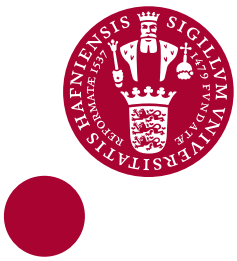

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Hybrids and the Flora of Thailand

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INTRODUCTION

This article, like its predecessor Chayamarit et al. (2007), is intended to stimulate discussion. If you have an alternative perspective, please write an article for submission to be published in a subsequent volume of TFB. It is intended that further such discussion-stimulating articles will be published from time-to-time.

Herein we highlight the surprising lack of records of plant hybrids in Thailand, suggest where hybrids may be sought and indicate that a range of techniques will be required to detect them. We do not comprehensively review plant hybridisation and, therefore, some topics such as hybrid zones (Harrison, 1993), introgression, species concepts and homoploid/polyploid speciation (Rieseberg, 1997) are not discussed in detail.

Hybrids are commonly listed in the Floras of many temperate countries (e.g. Stace, 2010) with the most commonly encountered, or at least recognised, hybrids in these regions being interspecific rather than intergeneric or interfamilial. Herein we focus on interspecific hybrids. Stace's (1975) compilation provides a useful, if now dated, review and indicates that at that time there were between 23,675 and 45,000 interspecific hybrids known worldwide, of which perhaps 50% were artificial (i.e. artificially induced). Certainly, spontaneous hybridisation appears common in nature, with perhaps 11% of the species listed in the Floras of the United Kingdom, Scandinavia, US Great Plains, US Intermountain and Hawaii being hybrids (Hegarty & Hiscock, 2005 quoting Ellstrand et al.'s, 1996 survey). Rieseberg (1997) uses the figure of 11% as the average value worldwide, whilst suggesting that it may represent a substantial underestimate. As there are likely to be somewhere between 10,250 (Middleton, 2003) and 12,550 species (Parnell, 2000) in the flora of Thailand a simple calculation suggests that there may be at least 1,126 to 1,375 interspecific hybrids in Thailand.

Ellstrand et al. (1996) found that spontaneous hybridisation is non-randomly distributed among taxa. This confirms the earlier finding of Stace (1975) who pointed out that the positive linear relationship between the number of species in a given family and the number of hybrids is broken

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by certain families. Stace (1975) highlighted the Betulaceae, Onagraceae, Orchidaceae, Pinaceae, Rosaceae and Salicaceae, as families wherein hybrids are conspicuously over-represented given the number of species. The reasons for the relatively high incidence of hybridisation in these families may be various and include, for example, certain cytological characters of the chromosomes (Onagraceae), deceptive pollination systems (many Orchidaceae, see below), or the relative abundance in areas that suffered severe disturbance during the Ice Age (Rosaceae). Following Ellstrand et al. (op. cit.) the Cyperaceae and Poaceae may be added to this list. So far the Orchidaceae (in part), Pinaceae, Rosaceae, Salicaceae and Cyperaceae have appeared in the *Flora of Thailand* series. Two of these families, the Pinaceae and Salicaceae, contain few species – thereby limiting the opportunities for hybridisation. The Rosaceae and especially the Cyperaceae and Orchidaceae accounts, by contrast, contain many species and a number of species-rich genera. The Orchidaceae account in the *Flora of Thailand* is, as yet, incomplete but in the sole part so far published only a very few hybrids (JP counted 2) are mentioned. No hybrids are mentioned in the Cyperaceae or Rosaceae accounts (though admittedly many of the species listed in the latter are introduced). For a more detailed consideration of the Orchidaceae and Cyperaceae, please see separate sections below. Therefore, although Stace's (1975) statement on these families may be true in general terms, it is not so far reflected in the *Flora of Thailand*. Indeed, when all the volumes of the Flora so far published are consulted the phenomenon of hybridisation is rarely mentioned with very few hybrids being recorded and those hybrids that are recorded not necessarily occurring in the most species rich families. Of course, some as-yet-unpublished family accounts will, almost certainly, mention hybrids because preliminary accounts of those families published elsewhere do so e.g. the Dipterocarpaceae (Pooma & Newman, 2001). There is, nevertheless, a stark contrast between the incidences of interspecific hybrids reported in the Floras of temperate regions and in the *Flora of Thailand*.

A similar situation exists for *Flora Malesiana* in which almost a third of the estimated 30,000 species have so far been treated but only 12 hybrids have so far been recorded, half of them in *Nepenthes* and *Potamogeton* (three each). Within the Rosaceae only a hybrid in *Fragaria* has been described. Obviously, further hybrids, though probably few in number, may be found in as yet untreated families. For example, although the Poaceae have not yet been treated in *Flora Malesiana* Goh et al. (2011) speculated on hybridisation in cultivated bamboos in SE Asia and described a natural intergeneric hybrid from Peninsular Malaysia.

There are also only a few reported hybrids in tropical America. The American palm genus *Attalea* has several reported natural hybrids (Glassman, 1999). Spontaneous and artificial hybrids are also known in cultivated ornamental palms (Hodel, 1992) and palms used as crops. For example the African oil palm, *Elaeis guineensis* Jacq., and an American congener, *Elaeis oleifera* (Kunth) Cortés, have been crossed in breeding programmes to obtain improved varieties (Hardon & Tan, 1969). In Asian palms, however, there are few or no examples of natural hybrids (A. Henderson, pers. comm.) and natural palm hybrids have not been reported for Thailand (A. Barfod, pers. comm). In another large family in tropical America, the Ericaceae, hybrids are rare if they occur at all (J.L. Luteyn, pers. comm.) and the reports that do exist are all based on intermediate morphologies without further tests (e.g. Sleumer, 1952; Middleton, 1991). In the Rosaceae there are reported hybrids in America. The high elevation tree genus *Polylepis* has at least four hybrids (Simpson, 1979), the high elevation herbaceous genus *Lachemilla* has at least three and *Rubus* has two reported hybrids from Ecuador (K. Romoleroux, pers. comm.). For the large family Araceae Tom Croat reports (pers. comm.) that:

"I can certainly assure you that in *Anthurium* and *Philodendron* many species have been hybridised. I found that nearly every species in a given section of *Anthurium* was capable of hybridizing although hybridisation between sections is rare. There seems to be evidence that natural hybrids also occur, especially in sect. *Porphyrochitonium* where there are anuploid series both higher and lower than the standard 2n=30 chromosomes which is at least indirect evidence that hybridisation has occurred. Natural hybrids have also been found in *Dieffenbachia* based on studies by Helen Young.

Alternatively in all my years of field work I have seen little evidence that extensive hybridisation occurs in the wild, rarely finding obvious intermediate collections in the vicinity of two distinct species. In *Philodendron* in the Guianas on the other hand there are a couple of rather obvious hybridisations. Joep Moonen has found two clear hybrids there and I too have seen a rather obvious hybrid at the Inselberg La Virginie. In *Anthurium* there is a case of what appears to be a rather obvious hybrid on St. Johns in the Virgin Islands where *A. selloum* K. Koch, described as a distinct species, [it] seems very obvious that it is a hybrid between *A. crenatum* and *A. cordatum*, the only two other species that occur there."

Finally, on the basis of decades of personal observations, it is clear that the paucity of written hybrid records for Thailand parallels the paucity of specimens of hybrids from Thailand (and other SE Asian countries) in herbaria.

In summary, the lack of specimens and paucity of records for hybrids in the *Flora of Thailand* and *Flora Malesiana* (and probably more widely in SE Asia and in the neo-tropics) is peculiar as hybrids are commonly encountered in temperate herbaria and are listed in the Floras of many temperate countries (*e.g*. Stace, 2010). More data are required to confirm whether this pattern in SE Asia and other tropical regions is real or an artefact of our poorer state of knowledge compared to temperate regions.

Hybridisation - some examples from the Orchidaceae and Cyperaceae.

a. Orchidaceae

The Orchidaceae account in the *Flora of Thailand* is as yet incomplete but it already seems clear that the confirmed/likely cases of hybridisation in this large family in Thailand are surprisingly few. Nevertheless, the known examples (though not consistently supported by solid empirical data) represent an interesting diversity of scenarios.

Hybrids often exhibit overall morphological intermediacy between the parental species and presumed F1 hybrids have been reported on a few occasions. The most thoroughly described cases are *Paphiopedilum appletonianum* (Gower) Rolfe × *Paphiopedilum callosum* (Rchb.f.) Stein, that Rolfe (1896) recorded from commercial importations of the putative parental species from Thailand, and *Sirindhornia mirabilis* H.A.Pedersen & Suksathan × *Sirindhornia monophylla* (Collett & Hemsl.) H.A.Pedersen & Suksathan that was recently recorded and illustrated from the province of Tak (Pedersen & Ormerod, 2009).

It is sometimes difficult to assess whether a newly proposed species is indeed a genetically distinct, self-reproducing entity, or whether the description simply covers hybrids (and possibly introgressants). One such case is *Cymbidium baoshanense* F.Y.Liu & Perner that was originally described from Yunnan (Liu & Perner, 2001) and recently collected in northern Thailand (Pedersen et al. unpubl.). Emphasizing its marked variability and overall morphological intermediacy between *Cymbidium lowianum* (Rchb.f.) Rchb.f. and *Cymbidium tigrinum* C.S.P.Parish ex Hook., Du Puy & Cribb (2007) considered it a hybrid between the latter two – a hypothesis that is supported by *C. baoshanense* closely resembling the artificial hybrid of the same parentage (Liu et al., 2009).

It has been proposed that introgressive or ancient hybridisation may have influenced genetic composition of *Paphiopedilum godefroyae* (God.-Leb.) Stein – a species endemic to peninsular Thailand. Compared to most other narrow endemics, the polymorphism of *P. godefroyae* is remarkable, and three differently distributed varieties are currently recognised (Cribb, 2011). It is a tempting thought that some of the variation has been generated by hybridisation. The taxon currently recognised as *P. godefroyae* var. *ang-thong* (Fowlie) Braem was originally described by Fowlie (1977) who considered his *Paphiopedilum* ×*ang-thong* Fowlie to be a natural hybrid swarm between *P. godefroyae* and *Paphiopedilum niveum* (Rchb.f.) Stein. The nearest known populations of *P. niveum* are, however, situated several hundred kilometres to the south of the Ang Thong islands, and the morphological evidence for hybridisation between *P. godefroyae* and *P. niveum* seems slim (Cribb, 1998). Furthermore, *P. godefroyae* is pollinated by milesiine hoverflies and *P. niveum* by the meliponine bee *Tetragonula testaceitarsis* (Bänziger et al., 2012). Vectorwise and geographically, introgressive hybridisation between *P. godefroyae* and *Paphiopedilum concolor* (Bateman) Pfitzer appears

more likely (Bänziger et al., 2012), and this possibility should be investigated further. Finally, the proposal of Cribb (1998) and others that *Paphiopedilum godefroyae s.l.* might be a species of hybrid origin also calls for an in-depth study. This could appropriately focus on the genetic relationships between *Paphiopedilum godefroyae*, *P. bellatulum* (Rchb.f.) Stein and *P. concolor*, as these taxa are all pollinated by milesiine hoverflies (Bänziger et al., 2012).

Most putative cases of hybridisation among Thai orchids do not occur as chance discoveries of clearly morphologically intermediate individuals; they more frequently appear in connection with close taxonomic studies of poorly resolved species complexes. For example, morphometric and AFLP data indicate some traditionally recognised species in *Geodorum* to be poorly separated – possibly, but not necessarily, due to recent hybridisation and introgression (Pedersen et al., in prep.).

b. Cyperaceae

In the Cyperaceae hybrids are frequently reported, especially in *Carex*, a genus comprising nearly 2000 species that is present in both tropical and temperate regions, including Thailand. Other widespread genera that are known to hybridise include *Eleocharis*, *Schoenus*, *Schoenoplectus* and *Trichophorum*; again, these are represented in the tropics, including Thailand. All the reported hybrids are between temperate taxa: for example over 40 *Carex* hybrids have been recorded in the British Isles (Jermy et al., 2007) where the total species complement is 71. No hybrids have been recorded between tropical taxa in these genera. There is one report of putative hybridisation in the pantropical genus *Mapania*, between *Mapania macrophylla* (Boeck.) H.Pfeiffer and *Mapania insignis* Sandwith (Koyama, 1967). This was subsequently discounted, however, with the specimens now being considered part of the range of variation in *M. macrophylla*. (Simpson, 1992).

Jermy et al. (2007) noted a whole range of potential pitfalls when attempting to recognise hybrids in Cyperaceae, especially when the characters are cryptic and contradictory or when the hybrid resembles one or other of the parents. It is these pitfalls that may have caused hybrids to be overlooked among the tropical taxa, especially when these taxa have been subject to much less detailed scrutiny than their temperate relatives.

Potential reasons for the dearth of records in the flora / Flora of Thailand

There are a number of potential reasons, not necessarily mutually exclusive, for the dearth of records for plant hybrids in Thailand and surrounding areas.

Firstly, hybrids may be genuinely scarce in Thailand (and SE Asia). If this is the case it may be due to real differences in biological processes in this region, or perhaps more generally in the tropics, vis a vis the temperate zone. Certainly, Ellstrand et al.'s (1996) survey of five floras also revealed a relatively low incidence of hybrids in the only tropical flora they surveyed (Hawaii). Ellstrand et al. (1996) admitted that whilst this low incidence might be a function of tropical floras in general they believed that it was more likely due to the fact that tropical floras have received less biosystematic attention than temperate ones. On the other hand there are many biological processes that may be different between tropical and the temperate zones and these may have an effect on the frequency of hybridisation. For example, hybrids may be rarer in tropical forests than in temperate regions because of more specialised pollination syndromes, sequential flowering, or the lower proportion of polyploidy (Kiew et al., 2003). It is also known that asexual reproduction (apomixis, autogamy), although rarely reported for tropical forests, may in fact be much more common (Kaur et al., 1978), again limiting the potential for hybridisation.

Secondly, hybrids may exist in similar proportions in Thailand as in temperate regions but have just not been detected due to a lack of biosystematic attention. This could be because collecting densities in Thailand are low (Parnell et al., 2003) and much lower than temperate regions.

Thirdly, it could be because knowledge of the morphological boundaries of species is poorer in Thailand than in temperate regions thereby making recognition of intermediacy, *i.e.*, hybrid recognition, tricky. Of course intermediacy does not always occur in hybrids (Rieseberg & Ellstrand, 1993; Thomasset et al., 2011). Hybrids can have parental

characters or intermediate characters. But there is no reason to presuppose that non-intermediacy is more common in the tropics than the temperate zone.

Fourthly, the distinctions between species in tropical floras are mainly based on morphological differences detected between herbarium specimens and not on observations of living plants. This may result in the recording of hybrids as separate species as long as differences are found. Of course the opposite may be possible, that the species concept applied in tropical regions is broader than that in temperate regions. Equally, the fact that many plant hybrids do not necessarily show distinct morphological differences may limit their detection.

Finally, as Ellstrand et al. (1996) pointed out, hybridisation is most common in certain families and, within those families, in certain genera. These genera tend to comprise species of outcrossing perennial herbs with reproductive modes such as permanent odd polyploidy, agamospermy or vegetative spread that act to stabilise hybridity. It is possible that such genera are rare in Thailand. On the other hand it is clear that some genera of tropical trees (Pooma & Newman, 2001) produce interspecific hybrids and so the potential poverty of genera of outcrossing perennial herbs may not be so much of a limiting factor.

Overall, it is likely that different explanations apply to different species and that no one single explanation is universally correct. Only a thorough search in appropriate areas for hybrids and an understanding of the process of their formation will enable the reasons underpinning the dearth of records of hybrids in Thailand to be discovered.

Where to search for hybrids?

Intuitively, it might seem as if hybrids would be worth seeking where large, rather than small, populations of very similar, phylogenetically closely related species are sympatric or parapatric. Rieseberg (1997) suggests, however, that hybridisation is most frequent in small or peripheral populations.

Stace (1975) points out that hybrids are often found in areas that are disturbed, where new habitats exist. Though such disturbance is often anthropogenically caused, other agencies capable of creating such conditions exist. They include 'ice-ages, fires, land-slips, damage by the sea, volcanic eruptions, sudden large scale attacks by predators or parasites and other natural catastrophes' (Stace, 1975) and also areas where introduced species occur (Abbott, 1992). It might be expected, therefore, that hybrids could be most easily searched for in anthropogenically disturbed areas in Thailand, in areas recovering from large scale environmental changes (*e.g.*, wasteground, roadsides, cleared farm-land, etc.), and where large numbers of introduced plant species occur. There are, obviously, a variety of areas in Thailand that meet these criteria. In terms of natural processes, however, there are other areas in Thailand and SE Asia where hybrids may commonly occur and where they should be sought. Two such regions stand out. They may both be suture zones *sensu* Swenson (2010).

The original debate on the existence of suture zones was tense (Short, 1969, 1970; Uzzell & Ashmole, 1970) and then the concept was 'ignored for nearly three decades' (Swenson, 2010) being largely revived by Hewitt's series of papers (*e.g.* Hewitt, 2001). In summary, suture zones bring into juxtaposition long-isolated lineages (Moritz et al., 2013) and, as originally defined (Remington, 1968), are geographic areas where multiple hybrid zones cluster – that is where hybrids may be more commonly encountered than elsewhere. Remington's (1968) original work focussed primarily on animals (birds) but can be applied to plants as well. Hewitt (1993 in Hewitt, 2001) suggests that suture zones are interfaces between regional biotas where many diverged genomes met and hybridised after the last Ice Age. More recently the concept of suture zones has been expanded to include the spatial clustering of phylogeographic breaks and the spatial clustering of hybrid zones (Swenson & Howard, 2005; Swenson, 2010) and, in the context of this paper, suture zones are not considered to be linked to the last Ice Age nor to be confined to animals. The core issue is that suture zones are areas where previously geographically isolated populations from multiple taxa come together in a particular geographic locality (Uzell & Ashmole, 1970) and hybridise.

In the tropics only a single suture zone has been confidently identified (Moritz et al., 2013). It

is likely, however, that others exist and in SE Asia two regions would appear to be prime candidates: they are the biogeographic, phylogeographic and ecotonal divide in the Isthmus of Kra region (Parnell, 2013) and a similar divide associated with Wallace's Line (Van Welzen, et al., 2011b). As the Isthmus of Kra falls within the area of the *Flora of Thailand* we suggest that it will be worthwhile searching for hybrids in that area. It may be, however, that the boundary in the Isthmus of Kra region is too substantial to allow for frequent hybridisation – the taxa may be too genetically distinct. Certainly, many northern genera do not venture south and many southern genera do not venture north of the boundary and intergeneric hybrids are generally rare. Further study of hybridisation at species level in the region is required.

There are probably other less well-known or well-defined biogeographic divisions in the *Flora of Thailand* area (Van Welzen et al., 2011a): these too would be worthy of further search for hybrids.

Equally, hybrids should probably be sought in other areas where ecotonal divisions occur and in any area where anthropogenic impact is substantial.

Finally, it is important that a broad range of techniques are used to detect hybrids. As Hegarty & Hiscock (2005) indicate, the application of molecular approaches, such as chromosome painting, DNA sequences and c-DNA microarrays, offers an opportunity to revolutionise the study of hybrid speciation. DNA markers of nuclear and plastid origin are often used to study the parental origins of hybrids (Rieseberg & Carney, 1998). Nuclear markers are biparentally inherited and can detect both parental contributions in a hybrid. If the hybrid is an F1 or of recent origin then the markers clearly show parentage (Hodkinson et al., 2002; Thomasset et al., 2011). Such markers can also be used to study introgression through various methods of assignment testing (Field et al., 2010; Thomasset et al., 2013). Plastid markers are usually maternally inherited in angiosperms and can be used to identify the maternal parent of hybrids and detect asymmetric hybridisation (Hodkinson et al., 2002; Field et al., 2010). Such techniques facilitate detection of plant hybrids, many of which may be cryptic and not show distinct morphological differences. Molecular markers have also detected ancient hybridisation events in a phylogenetic context (Wendel et al., 1995). In these cases hybridisation is the explanation for incongruent gene trees.

CONCLUSION

Implicit in this article is the assumption that the published work entitled 'Flora of Thailand' should reflect the flora of Thailand (*i.e.* the taxa, native and commonly introduced, that grow in Thailand), just as the Stace's 'Flora of the British Isles' (Stace, 2010) reflects the spectrum of taxa that grow in the British Isles. If further surveys show that hybrids are common in Thailand this raises a number of questions which include: why are hybrids not recorded in the Flora and should hybrids be recorded in the Flora? If, on the other hand, hybrids are rare then a whole raft of other interesting biological questions arise.

It is likely that an extensive literature search, especially in the non-Thai literature, specifically for interspecific hybrid records involving species that have accounts already published in the *Flora of Thailand* series would reveal any reports of hybridisation for these species outside of Thailand and so at least summarise the potential for the occurrence of hybrids in the flora.

In summary, further searches for hybrids will certainly add to our knowledge of the flora of Thailand, help in understanding the potential role of hybridisation in plant speciation in the region (see Rieseberg & Willis, 2007 for a discussion of this issue in general terms), and we hope that this paper will initiate debate on the status of hybrids vis a vis the *Flora of Thailand*. We believe that the lack of recorded hybrids shows the value of the *Flora of Thailand* series. These volumes must be the starting point for any future studies that investigate the systematics of the species in more detail. It is at that point that researchers may realise that some plants, currently recognised as distinct species, are in fact of hybrid origin.

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